An Early Triassic (Dienerian) microgastropod assemblage from the Salt Range, Pakistan and its implication for gastropod recovery from the end-Permian mass extinction

Nützel, A ; Ware, D ; Bucher, H ; Hautmann, M ; Roohi, G ; Ur-Rehman, K ; Yaseen, A

Abstract: A single limestone sample from the Early Triassic (late Dienerian) of the Salt Range in Pakistan has yielded numerous small gastropods (smaller 2 mm), few bivalves and abundant ammonoids. The limestone is interpreted as a tempestite. Many of the gastropods are extremely well-preserved including protoconch preservation and micro-ornaments. Five species of gastropods are present: (1) isolated larval shells representing a neritimorph taxon of the family Trachyspiridae, (2) early juvenile and larval specimens of the caenogastropod Strobeus pakistanensis, (3) the new caenogastropod species Coelostylina hydrobiformis Nützel Ware, (4) the new heterobranch genus and species Eographis microlineata Nützel Ware representing the earliest occurrence of the extant family Hyalogyrinidae (Valvatoidea), (5) the heterobranch Sinuarbullina sp., a genus which originates in the Early Triassic and has also been reported from China, Spitsbergen and the US. Three genera (trachyspirid, Strobeus and Coelostylina) represent survivors from the end-Permian mass extinction whereas Eographis and Sinuarbullina have their earliest known occurrence in the Early Triassic. Eographis is the first Early Triassic genus for which coaxial larval heterostrophy is shown. Together with the Devonian genus Palaeocarboninia and the Carboniferous genus Heteroaclisina, it witnesses a high age of Ectobranchia (living families Hyalogyrinidae, Valvatidae, Cornirostridae and Xylodisculidae). This supports the assumption that this group is the first extant offshoot of the Heterobranchia. The studied assemblage is strongly dominated by Strobeus pakistanensis. The small size of the gastropods reflects their ontogenetic stage (early juvenile and larval shells) as well as a small adult size in some of the species. Most of the present gastropods had planktotrophic larval development providing further evidence against the hypothesis that the end-Permian mass extinction event selected against larval planktotrophy. Failure to grow to a larger size or to perform metamorphosis suggests unfavourable living conditions in the source community probably due to oxygen deficiency prior to transport by storm. Size sorting is seen as less likely because the limestone is poorly sorted with relatively large ammonoids being present in considerable numbers.The studied sample yielded also three bivalve taxa amongst them two species representing the genera Leptochondria and Crittendenia. • Key words: Gastropoda, Bivalvia, Early Triassic, Recovery, end-Permian extinction, protoconchs.

DOI: https://doi.org/10.3140/bull.geosci.1682

Nützel, A; Ware, D; Bucher, H; Hautmann, M; Roohi, G; Ur-Rehman, K; Yaseen, A (2018). An Early Triassic (Dienerian) microgastropod assemblage from the Salt Range, Pakistan and its implication for gastropod recovery from the end-Permian mass extinction. Bulletin of Geosciences:56-70.
DOI: https://doi.org/10.3140/bull.geosci.1682

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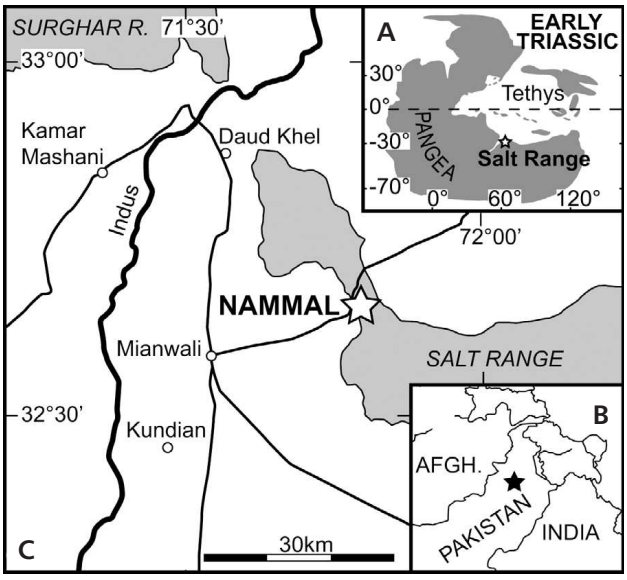


Figure 1. Locality maps (modified from Ware *et al.* in press). • A – palaeogeographical map of the Early Triassic with the palaeoposition of the Salt Range (modified from Brayard *et al.* 2006). • B – map of Pakistan with position of the studied area (black star). • C – location map of Nammal Nala in the Salt Range (modified after Brühwiler *et al.* 2012).

The Salt Range hosts important Permian-Triassic marine sections which have yielded abundant ammonoids that provide a well-studied stratigraphic framework (*e.g.* Waagen 1895; Brühwiler *et al.* 2010, 2011, 2012; Ware *et al.* 2015, in press). Kaim *et al.* (2013) provided the first detailed study of Early Triassic (Smithian/Spathian) gastropods from the Salt Range. These authors reported five gastropod species: the bellerophontoid *Warthia hisakatsui* Murata, 1981, the neritimorph *Naticopsis* sp., two new species representing the caenogastropod genus *Strobeus* (*S. batteni* and *S. pakistanensis*) as well as the caenogastropod *Coelostylina* sp. Most of these species were present with more or less fully-grown individuals in the centimetre-size range except for *Coelostylina* sp. and early juveniles of the genus *Strobeus*. In the course of the study of Dienerian ammonoids from the Salt Range, one of us (DW) discovered mass accumulations of tiny (< 2 mm) gastropods in the matrix between the ammonoids. These highly abundant gastropods are very well preserved and are reported in the present contribution.

Geological setting

The Salt Range is a low mountain range situated about 150 km SSW of Islamabad (Fig. 1B). In the Early Triassic, it was situated in Southern Tethys, at a palaeo-latitude of *ca.* 30° S (Fig. 1A). The Salt Range constitutes a key locality for the study of Early Triassic marine faunas due to its extensive outcrops of highly fossiliferous marine sediments. Nammal Nala is one of the classical localities for the study of the Permian-Triassic of the Salt Range and has been extensively studied by *e.g.* Kummel (1966), Kummel & Teichert (1970), Guex (1978), Hermann *et al.* (2011a), Brühwiler *et al.* (2012), Wasmer *et al.* (2012) and Ware *et al.* (in press). It is a small canyon situated *ca.* 25 km ENE of Mianwali (Fig. 1A).

In the Salt Range, the Early Triassic is represented by the Mianwali Formation, a *ca.* 120 m thick succession of limestone and siliciclastic marine sediments. This formation unconformably overlies the late Permian Chiddru Fm. In Nammal Nala it is conformably overlain by the terrestrial Middle Triassic Tredian Fm. The Mianwali Fm. is usually subdivided into seven units (*e.g.* Guex 1978) of which only the stratigraphically third, the Ceratite Marls (middle Dienerian–early Smithian), is relevant here. In Nammal Nala, the Ceratite Marls represent a *ca.* 25 m thick shale interval with intercalated limestone and sandstone beds. Limestone beds are abundant in the lower third of the unit which is middle to late Dienerian in age. Limestone beds become rare in the two uppermost thirds of the units which are early Smithian in age while sandstone beds progressively become more abundant in the upper third. Hermann *et al.* (2011a, b; 2012a, b) showed that the middle to upper Dienerian part of the Ceratite Marls in Nammal recorded a local peak of anoxia. Romano *et al.* (2013) showed that it also coincided with a peak in temperature.

In addition to ammonoids (Ware *et al.* in press) and gastropods (partly described herein), bivalves are the most abundant fossils of the Ceratite Marls. In Nammal Nala, *Claraia aurita* (= *Claraia concentrica*) is very abundant in the lowermost part of the section but disappears abruptly *ca*. 0.8 m above the base of the Ceratite Marls. In contrast, *Leptochondria* and *Bakevellia* occur in high abundances throughout the Ceratite Marls. An additional bivalve taxon is represented by thin circular shells that might represent diagenetically flattened left valves of *Crittendenia*.

Material and methods

The gastropods described here all come from a single sample (NAM101d) from Nammal Nala, about 6 m above the base of the Ceratite Marls. The rock sample was crushed with a hammer on a steel plate and resulting rock gravel and powder was washed and sieved at a mesh size of 0.5 mm. Part of the dried residue was picked quantitatively under a stereomicroscope. The best-preserved specimens were sputter-coated with gold and photographed under a SEM. One thin section was produced from the sample. The specimens and the thin section are housed at the Paläontologisches Institut und Museum, Universität Zürich (abbreviated PIMUZ).

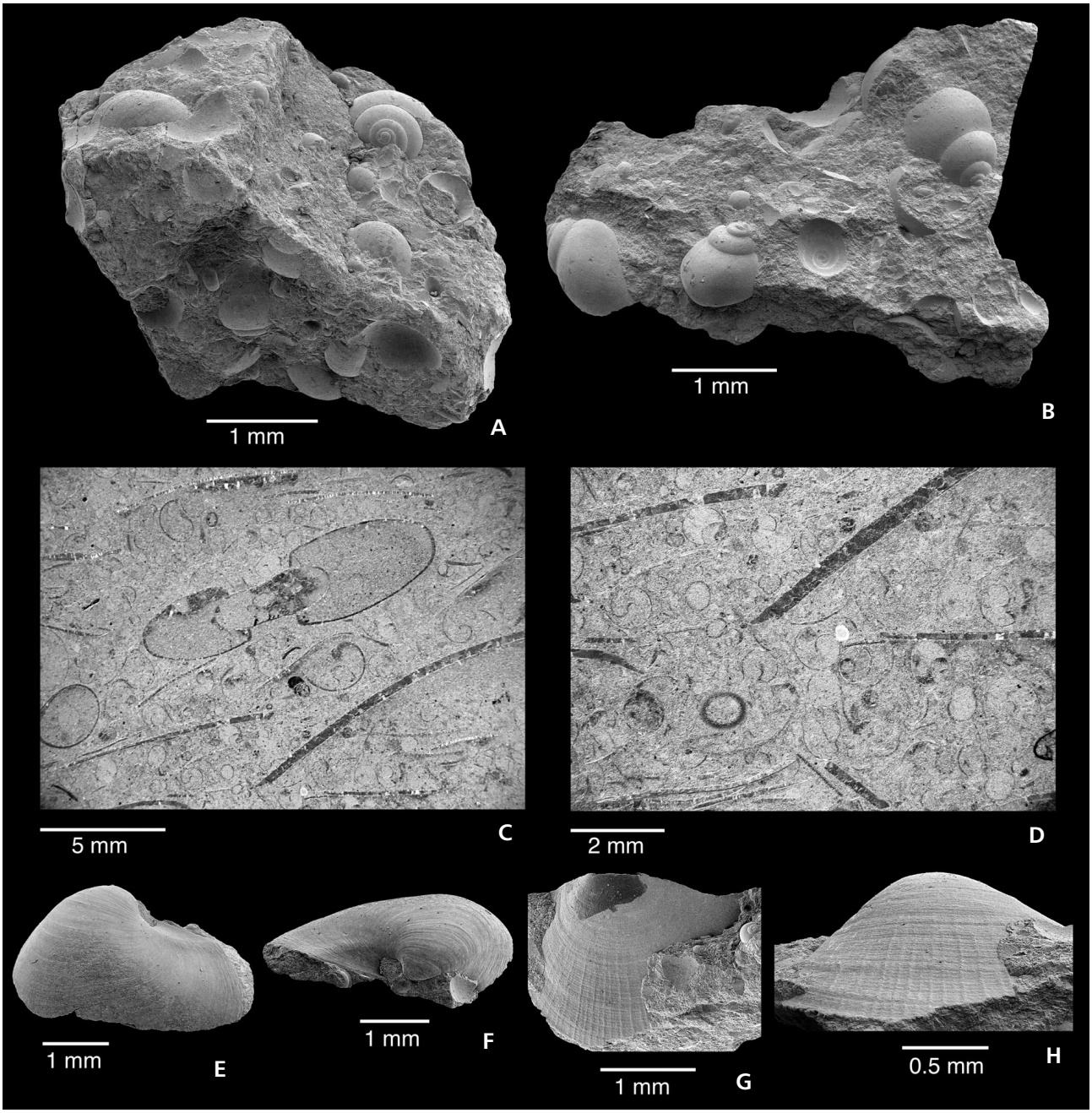


Figure 2. A, B • rock fragments showing several gastropods namely *Strobeus pakistanensis*; A – PIMUZ 32888, 32889; B – PIMUZ 32908–32910. • C, D – thin section of fossiliferous source rock of studied fauna; mollusc packstone with numerous gastropods, an ammonoid (C) and unidentified filaments probably representing bivalve or ammonoid fragments (D), PIMUZ 32945. • E, F – unidentified heteroconch species, PIMUZ 32937. • G, H – *Leptochondria* cf. *albertii/curtocardinalis*, PIMUZ 32931.

The exact stratigraphic position of the studied sample is indicated in Ware *et al.* (in press, fig. 4). It is late Dienerian in age and belongs to the *Kingites davidsonianus* Regional Zone of Ware *et al.* (in press) and zone DI-10 of Ware *et al.* (2015). Similar microgastropod assemblages were found in the middle and late Dienerian of several localities in the Salt Range as well as in Spiti (Himachal Pradesh, India). Microgastropods from the present sample are described here because of their excellent preservation. Like most limestone beds in the lower third of the Ceratite Marls from Nammal, sample NAM101d comes from a tempestite layer with highly variable facies. The base of the bed is usually a packstone with numerous ammonoids, bivalves and microgastropods, while its top is a floatstone with few ammonoids and rare bivalves and microgastropods. The facies of the sampled bed varies considerably laterally even

across short distances (decimetres). The microgastropods described here come from the basal part of the bed, with numerous densely packed tiny gastropods (< 2 mm; Fig. 2A–D). The numerous ammonoids are imbricated, the large ones are usually partially broken and large ammonoid shell fragments are frequent. The ammonoid fauna from this zone is described in detail in Ware *et al.* (in press). It is dominated by *Koninckites khoorensis* and *Kingites davidsonianus* is not rare. Other ammonoid species are very rare.

The paucispecific bivalve fauna found in larger rock fragments of the limestone bed (*i.e.* not crushed as described above) comprises three different taxa: (1) a weakly costellate *Leptochondria* similar to *L. albertii* and *L. curtocardinalis* (see discussion *in* Hautmann *et al.* 2013, p. 275), (2) poorly preserved left valves of *Crittendenia* and (3) a small heteroconch bivalve with unknown internal morphology, which bears some external resemblance to the Palaeozoic *Cypricardella* Hall, 1856 (*e.g.* Girty 1927, pl. 25, figs 60–78). The crushing method applied for preparation of the gastropods (see above) likely destroyed to a higher degree shells that are less isometric than gastropods, which might explain why bivalves are underrepresented in sample material which was prepared this way. However, two small bivalve specimens have been found among the small-sized gastropods, which can be assigned to *Leptochondria* cf. *albertii/curtocardinalis* (Fig. 2G, H) and the unidentified heteroconch species (Fig. 2E, F) described above.

Results

The studied limestone sample is highly fossiliferous with densely packed tiny gastropods (< 2 mm) (Fig. 2A–D). It is a packstone with gastropods, bivalves and ammonoids. The crushed rock produced thousands of gastropod specimens representing five species. The gastropods are present as early juvenile specimens of usually larger growing species as well as small growing species and isolated larval shells. Juvenile *Strobeus pakistanensis* Kaim, Nützel, Hautmann & Bucher, 2013 is by far the most abundant gastropod species forming more than 90% of the assemblage. Ammonoid and bivalve fragments are also present in the sample prepared by crushing but less abundant. However, a thin section shows that larger shell fragments of ammonoids and/or bivalves are common. The shell material is entirely recrystallized (aragonite to calcite). When breaking the rock sample, the fractures commonly formed along the fossil shells exposing superbly preserved specimens in great detail. The preparation (by crushing) preferably exposes round, isometric fossils and thus gastropods are overrepresented whereas flat objects such as bivalves may be underrepresented. On the other hand, both isolated fossils and thin section suggest that gastropods are by far the most abundant group present in the rock sample.

Systematic Palaeontology

This published work and the nomenclatural acts it contains have been registered in ZooBank: *http://zoobank.org/References/D4BA361F-D0FF-476F-8425-B887D8616B0C*. The classification used herein is based on Bouchet *et al.* (2017).

Class Gastropoda Cuvier, 1797
Order Neritimorpha Koken, 1896
Superfamily Neritoidea Rafinesque, 1815
Family Trachyspiridae Nützel, Frýda, Yancey & Anderson, 2007

Trachyspiridae gen. et sp. ind.
Figure 3

Material. – Four specimens (PIMUZ 32886, 32912, 32924, 32932) from sample NAM101d, from Nammal Nala, about 6 m above the base of the Ceratite Marls (Ware *et al.* in press), Salt Range Pakistan, Early Triassic.

Description. – Shell broad; a larval shell fragment is 0.8 mm wide; a partly exposed larval shell comprising about three whorls is 0.9 mm high; rapidly expanding convex whorls with pending profile with periphery low on whorls near suture; whorls adpressed in a narrow subsutural zone; embryonic shell egg-shaped, smooth somewhat less than one whorl with a diameter of 0.14 mm and a diameter of first whorl of 0.17 mm; following larval whorls with numerous narrow, collabral axial ribs; ribs strongly sinuous, strongly prosocyrt on visible part of larval whorls with zenith low on whorls; ribs forming a pronounced opisthocyrt sinus on base of larval whorls; in addition a non-collabral micro-ornament of fine spiral threads converging at mid-whorl is present on early larval whorls; teleoconch unknown.

Remarks. – Neritimorph larval shells with sinuous axial ribs have been reported repeatedly from the Late Palaeozoic (Kues & Batten 2001 as *Lunuluzona*; Hua Zhang & Erwin 2002 as *Naticasinus*; Bandel 2002a as *Naticopsis*; Nützel *et al.* 2007). Interpretations as a small-sized pleurotomarioid (Kues & Batten 2001, Hua Zhang & Erwin 2002, Kues *et al.* 2004) have been refuted by Nützel *et al.* (2007) who found this type of larval shell conjoined with a teleoconch with knobby, spiny ornament representing the genus *Trachyspira*. Meanwhile, it was also found in typical *Trachydomia* shells (AN, personal observation) – a widespread late Palaeozoic genus which is close to *Trachyspira*. Kaim (2009) reported this type of larval shell from the

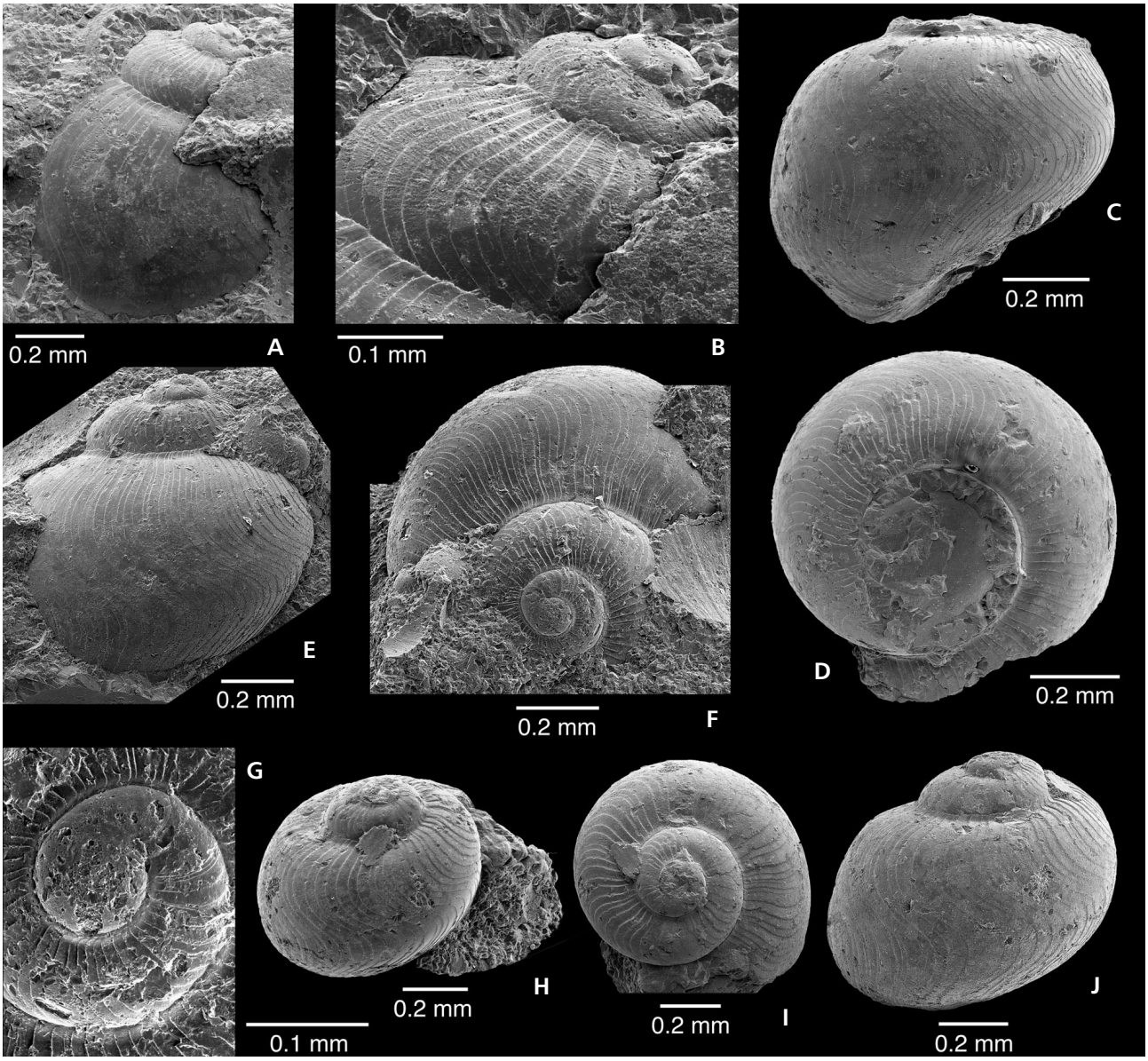


Figure 3. Trachyspiridae gen. et sp. ind.; A, B – PIMUZ 32886; C, D – PIMUZ 32912; E–G – PIMUZ 32924; H–J – PIMUZ 32932.

Early Triassic (early Dienerian) of Far East Russia (Abrek Bay). It is also present in the Smithian of the Western U.S. *i.e.* in the fauna from the Sinbad Limestone, Utah (AN, personal observation) that has been studied by Batten & Stokes (1986). Bandel (2007) reported this type of larval shell from several Late Triassic neritimorph genera from the St. Cassian Formation (North Italy) which were placed in Naticopsidae by this author. Thus, the neritimorph group having this characteristic type of larval shell is now known from the Carboniferous to the Late Triassic and had a global distribution. Thus, this neritimorph group survived the end-Permian mass extinction and there are now several reports from the Early Triassic.

Subclass Caenogastropoda Cox, 1960
Superfamily Soleniscoidea Knight, 1931
Family Soleniscidae Knight, 1931
Genus *Strobeus* de Koninck, 1881

Type species. – *Strobeus ventricosus* de Koninck, 1881, Carboniferous, Belgium.

***Strobeus pakistanensis* Kaim, Nützel, Hautmann & Bucher, 2013**
Figures 2A, B, 4

2005 *Strobeus* sp. – Nützel 2005, p. 441, fig. 7 left.

* 2013 *Strobeus pakistanensis* sp. nov. – Kaim *et al.*, p. 511, fig. 6a, b, f–h, j–l.

Material. – Numerous specimens (*ca*. 30 specimens studied with SEM: PIMUZ 32880, 32884, 32885, 32887–32890, 32893–32910, 32913–32915, 32917, 32918, 32920) from sample NAM101d, from Nammal Nala, about 6 m above the base of the Ceratite Marls (Ware *et al.* in press), Salt Range Pakistan, Early Triassic.

Description. – Only larval and juvenile specimens are at hand; largest specimen comprising 5–6 whorls, 1.7 mm high, 1.1 mm wide; shell bulbous-fusiform with dome-shaped, blunt but distinctly elevated spire; protoconch bulbous, consisting of about 4 rapidly increasing, distinctly convex whorls; initial whorl tightly coiled with a diameter of 0.11–0.14 mm, without ornament; following larval shell of about 3–4 whorls, embracing at periphery; entire protoconch 1–1.2 mm high, 0.9 mm wide; larval whorls ornamented with extremely fine, irregular ornament of chevron-like axial threads only visible in extremely well-preserved specimens at high magnification; larval shell ends at faint orthocline line where micro-ornament ceases (marked with arrows in Fig. 4B, E–H); teleoconch smooth with orthocline growth lines and with whorls higher than in larval shell; teleoconch whorls slightly adpressed; base evenly rounded, anomphalous.

Remarks. – We have at hand thousands of larval or early juvenile shells with a maximum height of 1.7 mm from the single studied sample. They closely resemble the juvenile shell of *S. pakistanensis* (3.3 mm high) which was illustrated by Kaim *et al.* (2013, fig. 6f–h, j–l). However, this shell appears to be entirely smooth and lacks the axial micro-ornament present in our material. It is likely that this ornament is not preserved in the material studied by Kaim *et al.* (2013). The holotype of *S. pakistanensis* is a rather large specimen (18.8 mm high) with worn early whorls so that it is not entirely sure – although likely – whether the mentioned larval and early juvenile specimens represent this species. *Strobeus pakistanensis* was first reported from the upper Smithian of the Salt Range (Kaim *et al*. 2013). The present small specimens from the Salt Range resemble *Strobeus shigetai* Kaim, 2009 from Early Triassic of Primorye but differ in having a much blunter apex and in being more bulbous. *Strobeus shigetai* has the same type of axial micro-ornament that is present on the early whorls of the specimens studied here. However, this ornament was interpreted as being on the teleoconch by Kaim (2009); by contrast, it is considered a larval shell ornament herein. It seems to be possible that this ornament represents also a larval ornament in *Strobeus shigetai*. It is obvious that *Strobeus pakistanensis* and *S. shigetai* are closely related as is suggested by its general shape and the characteristic micro-ornament of the early whorls – it is also present in soleniscoid species from the Smithian Sinbad Limestone of Utah (AN own observation). Orthostrophic caenogastropod larval shells that are smooth or only weakly ornamented have been reported for late Palaeozoic soleniscids by Nützel & Hua Zhang (2005). These species have tightly coiled initial whorls as is also the case for the present *Strobeus* species.

The generic identity of *Strobeus pakistanensis* and *S. shigetai* as well as other similar species is not beyond doubt – the type species of *Strobeus* has a thick and continuous inductura (Knight 1941) which is absent or not preserved in the mentioned Early Triassic taxa. Moreover, the early whorls including the protoconch have not been reported for the type species of *Strobeus*. The Late Palaeozoic species which have been assigned to *Strobeus* by Bandel (2002a) have an openly coiled initial whorl and this is not the case in *Strobeus pakistanensis* and *Strobeus shigetai*. The status of this character is unknown for the type species of *Strobeus*. Therefore, the generic identity of these Early Triassic species and those from the late Palaeozoic as reported by Bandel (2002a) remains open.

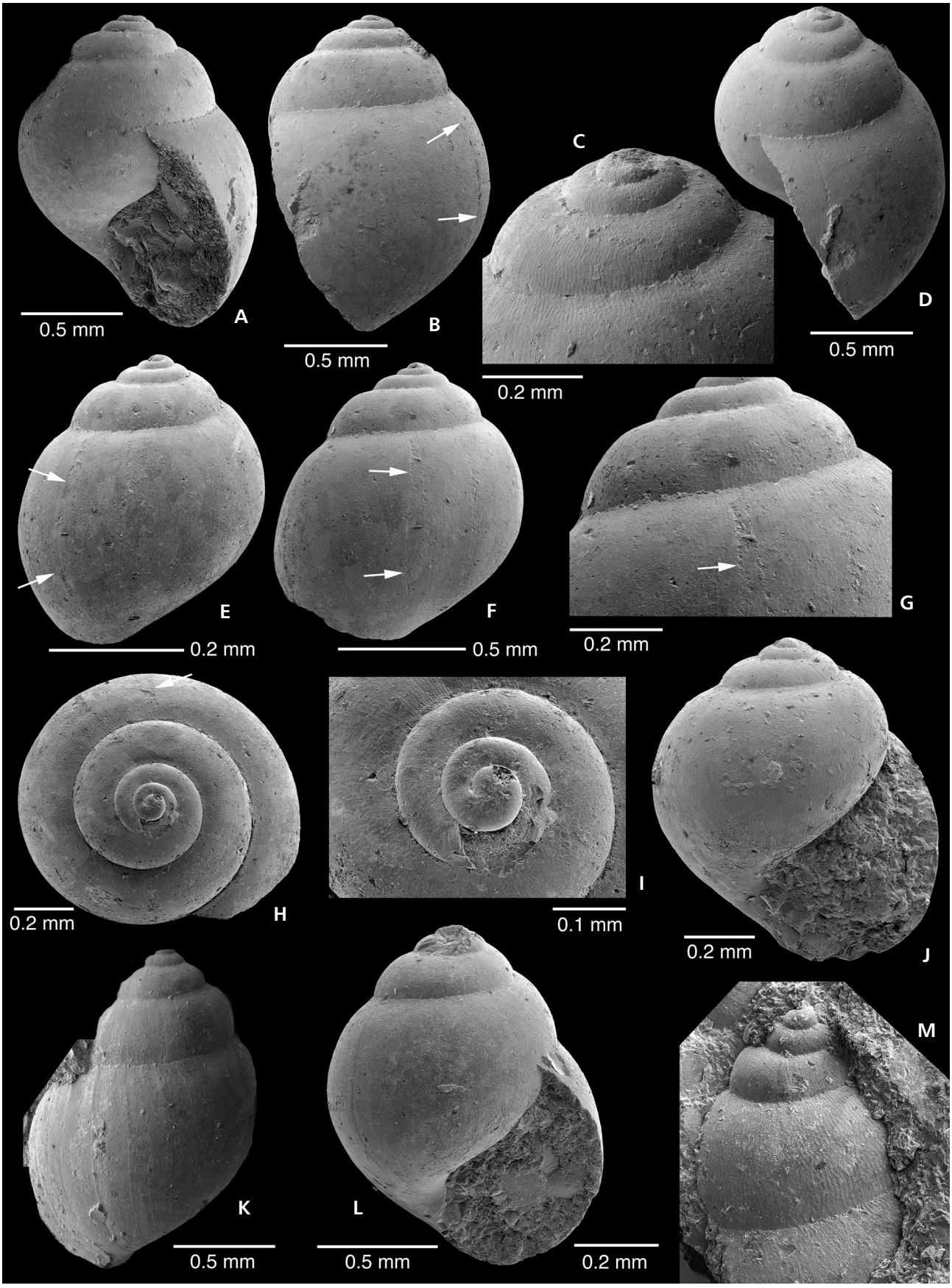
The present specimens of *Strobeus pakistanensis* have a small diameter of the initial whorl of 0.12–0.14 mm followed by about three whorls which are interpreted here as larval shell that ends at a faint line forming the border to the inferred teleoconch (marked with arrows in Fig. 4B, E–H). These dimensions suggest larval planktotrophy for this species (see Nützel 2014). With a height of up to 1.2 mm, the protoconch of *Strobeus pakistanensis* is rather large. However, there are several reports of larval shells in this size range from the Late Palaeozoic to early Mesozoic including examples representing Soleniscidae in which *Strobeus* is currently placed (Nützel & Mapes 2001, Mapes & Nützel 2009, Nützel 2014).

Superfamily unknown
Family Coelostylinidae Cossmann, 1909

Genus *Coelostylina* Kittl, 1894

Type species. – *Melania conica* Münster, 1841, Carnian (Late Triassic), Cassian Formation, northern Italy.

Figure 4. *Strobeus pakistanensis*; A–D – PIMUZ 32915; E–I – PIMUZ 32913, arrows indicating presumed end of larval shell; J – PIMUZ 32907; K – PIMUZ 32898; L – PIMUZ 32893; M – PIMUZ 32880.


A
0.5 mm
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C
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E
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H
0.2 mm
I
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0.2 mm
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0.5 mm
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M

***Coelostylina hydrobiformis* Nützel & Ware sp. nov.**
Figure 5

LSID. urn:lsid:zoobank.org:act:24095F5E-D50B-45E8-A0B3-18F59AAA66A0

? 2013 *Coelostylina* sp. – Kaim *et al.,* p. 512, fig. 7.

Types. – Holotype (PIMUZ 32926) and 12 paratypes (PIMUZ 32882, 32891, 32892, 32922, 32925, 32927, 32930, 32935, 32938, 32939, 32941, 32944).

Etymology. – After the modern gastropod genus *Hydrobia* which resembles the new species in shell shape.

Type horizon and locality. – Early Triassic, late Dienerian, from sample NAM101d, from about 6 m above the base of the Ceratite Marls (Ware *et al.* in press). Salt Range Pakistan, Nammal Nala.

Material. – See types.

Diagnosis. – Shell small, turbinid-hydrobiform; whorls strongly and evenly convex with periphery at about mid-whorl; sutures deep; first 2.5 whorls smooth (probably larval shell), later whorls with strengthened, strongly opisthocyrt growth-lines and spiral rows of minute pits; base evenly convex.

Description. – Shell high-spired, turbinid-hydrobiform, apical angle 35°–40°; largest studied shell consist of more than 4 whorls, 0.9 mm high, 0.7 mm wide; embryonic whorl not sufficiently preserved to infer termination; initial whorl has diameter of 0.12 mm to 0.16 mm; whorls strongly and evenly convex with periphery at about mid-whorl; sutures deep; first 2.5 whorls smooth, later whorls with strengthened, strongly opisthocyrt growth-lines and at least 3 spiral rows of minute pits; base evenly convex, with a blunt edge at transition to whorl face in the most mature specimen studied.

Discussion. – *Coelostylina hydrobiformis* sp. nov. is the first nominate species of Induan age assigned to the genus *Coelostylina*. The first 2.5 smooth whorls probably represent a simple larval shell of the planktotrophic type whereas later whorls, probably representing the teleoconch, have strong growth-lines and tiny pits – both are absent in the first 2.5 whorls. The tiny pits arranged in several rows have not been reported from any other small smooth-shelled gastropod species from the Early Triassic except of *Coelostylina* sp. as reported by Kaim *et al.* (2013) from a rock sample most likely derived from the Upper Ceratite Beds of Chideru, Pakistan (probably Mittiwali Member of Mianwali Formation, ?early Smithian, Early Triassic). The present shells are probably conspecific with *Coelostylina* sp. as reported by Kaim *et al.* (2013). However, Kaim *et al.* (2013) reported the presence of faint spiral lirae in their material (Kaim *et al*. 2013, fig. 7c) whereas this feature is absent in the present material.

Coelostylina hydrobiformis sp. nov. resembles several Triassic species which have been assigned either to the genus *Coelostylina* or the similar genus *Omphaloptycha*. However, many of these species are poorly known and features such as growth-line patterns as well as early ontogenetic shells have not been reported (some of them may be even *nomina dubia*). Moreover, spirally arranged pits are absent or unknown from nearly all of these species. Spirally arranged micro-pits have been reported for *Coelostylina brevissima* (Kittl, 1894) from the Ladinian Marmolada Limestone by Böhm (1895) and for *Coelostylina solida* (Koken, 1892) (*in* Wöhrmann & Koken 1892) from the Carnian of the South Alps by Broili (1907). Both species are much broader and have less convex whorls than the present species. A new *Coelostylina* species from the Anisian of Romania has also spirally arranged pits (Nützel *et al.* 2018). However, it is much larger, has a deeper suture and the growth lines are straight instead of prosocyrt.

Coelostylina sp. from the Early Triassic of Primorye, Far East Russia (Kaim 2009) is more slender and has a more acute apex. *Coelostylina costata* Batten & Stokes, 1986 from the Smithian Sinbad Limestone of Utah, USA has prominent axial ribs. *Coelostylina virginensis* Batten & Stokes, 1986 from the same formation has much less convex whorls and a more acute shell shape. *Coelostylina werfensis* Wittenburg, 1908 from the Early Triassic Werfen Formation of the Alps is much more high-spired. Moreover, this species is based on steinkern material and thus hardly comparable. *Pseudomurchisonia kokeni* Wittenburg, 1908 from the same formation has a subsutural shoulder and sinus, both features are absent in *Coelostylina hydrobiformis* sp. nov. and *Omphaloptycha schmidti* Assmann, 1924 from the Rötdolomit of Poland (probably Spathian/Anisian) is similar but has less convex whorls and shallower sutures; its growth-line pattern is unknown. *Omphaloptycha ahlburgi* Assmann, 1924 and *O. ecki* Assmann, 1924 from the Anisian Muschelkalk of Poland are more slender and have straight growth lines. *Omphaloptycha acuminata* Assmann, 1924 from the Diploporenendolomit (Anisian, Muschelkalk) of Poland is more slender and its base is demarcated from the whorl face by a rounded edge; its growth-line pattern is unknown.

Few Late Palaeozoic species have been assigned to *Coelostylina*. The Late Permian *Coelostylina gibsoni* Brown, 1839 from England (see Hollingworth & Barker 1991) is much more high-spired and slender and it has more convex whorls. A micro-punctation has not been

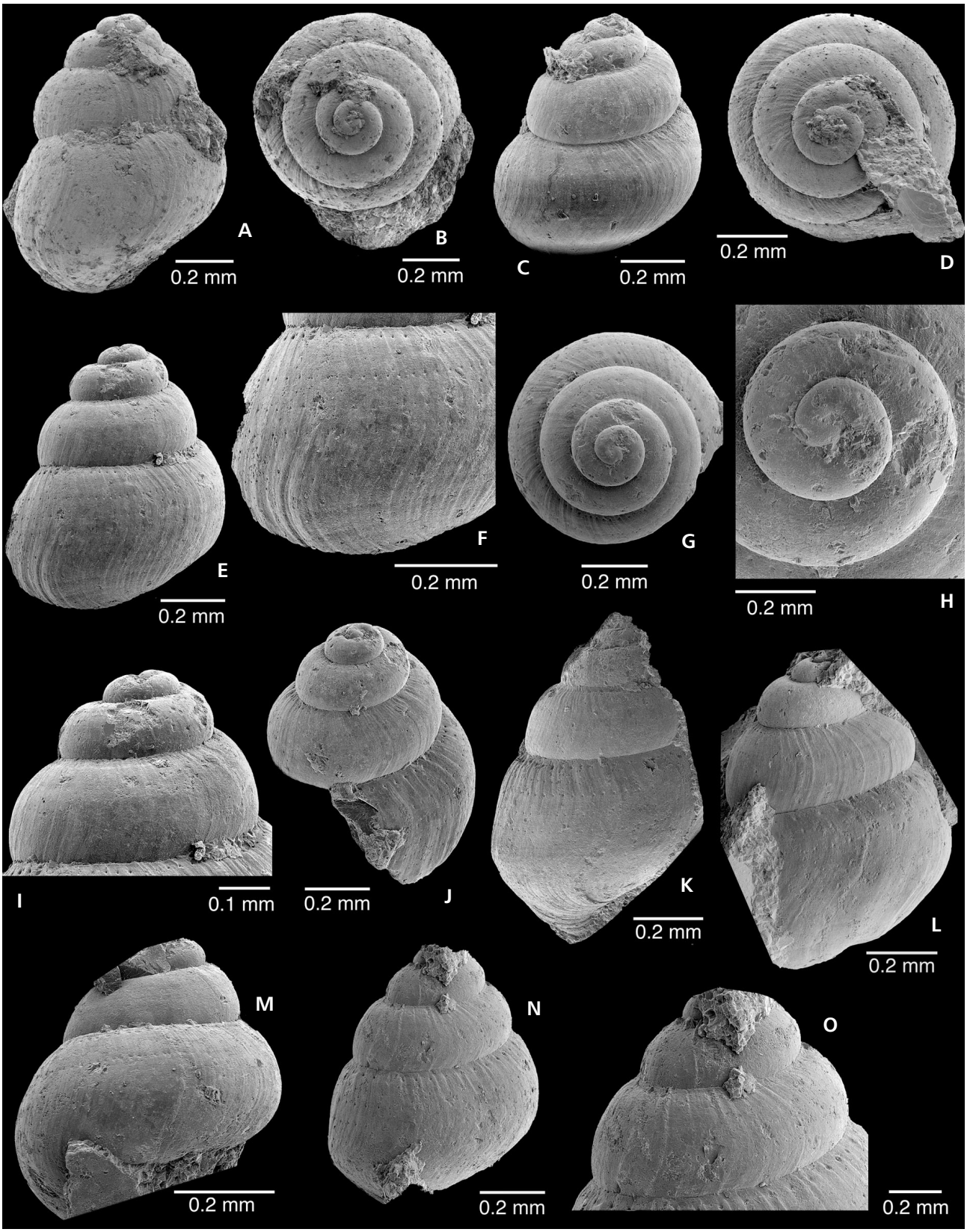

Figure 5. *Coelostylina hydrobiformis* sp. nov.; A, B – paratype, PIMUZ 32891; C, D – paratype, PIMUZ 32892; E–J – holotype, PIMUZ 32926; K – paratype, PIMUZ 32927; L – paratype, PIMUZ 32935; M – paratype, PIMUZ 32941; N, O – paratype, PIMUZ 32922.

reported for it and its protoconch is unknown. Batten & Stokes (1986) reported a single steinkern from the Smithian Sinbad Limestone (Utah, USA) as *Coelostylina* cf. *angulifera* (White, 1874). This specimen is much broader than *Coelostylina hydrobiformis* sp. nov. and has an angulated whorl profile. Originally *Macorcheilus angulifera* White, 1874 was reported from the Carboniferous of the USA and was later placed in the genus *Girtyspira* (Yochelson & Saunders 1967).

Subclass Heterobranchia Burmeister, 1837
Grade "Lower Heterobranchia"
Superfamily Valvatoidea Gray, 1840
Family Hyalogyrinidae Warén & Bouchet, 1993
(*in* Warén *et al.* 1993)

***Eographis* Nützel & Ware gen. nov.**

LSID. urn:lsid:zoobank.org:act:BBBF03A1-B262-4ED4-9A17-9C380FC4E805

Type species. – *Eographis microlineata* sp. nov.

Etymology. – Early (Eos: Greek goddess of the dawn) precursor of the modern genus *Graphis* Jeffreys, 1867.

Diagnosis. – Valvatoid with a tofanellid larval shell *i.e.* with coaxial heterostrophy which is largely smooth except for axial wrinkles in its early portion; teleoconch acutely trochiform; teleoconch whorls evenly convex, ornamented with fine axial lirae and finer spiral lirae.

Description. – As for *Eographis multilineata* sp. nov., type species of *Eographis* which is monotypic at present.

Discussion. – *Eographis* is so far a monotypic genus and it may be asked whether the description of genera comprising only a single species is justified or desirable. A database of all Triassic gastropods (Nützel unpublished) indicates that almost 40% of all Triassic gastropod genera are monospecific. If a species has a character combination that does not fit an already described genus, the erection of a new monotypic genus is warranted and placement in a previously described genus could even be misleading. The high number of monospecific genera reflects the incompleteness of the fossil record. Monospecific genera are also the result of a lagerstätten-effect. For instance, many genera from the Late Triassic St. Cassian Formation are monospecific because of the exceptional good preservation which facilitates the observation of characters that are normally not preserved (such as protoconch characters). Without such a good preservation, the species would probably be placed in genera with convergent teleoconch morphology or poorly known type species.

Eographis differs from the modern genus *Graphis* Jeffreys, 1867 by having finer more densely spaced axial threads and in being broader. Recent *Graphis* species are very slender to needle-shaped and have much coarser axial ribs (*e.g.* Bandel 2005). *Eographis* gen. nov. resembles the genus *Racheliella* Nützel, 2018 (Mathildoidea), recently described from the from the Late Triassic St. Cassian Formation (N Italy), by having a similar protoconch and by lacking strong ornament on the teleoconch. However, the ribs on the protoconch are much weaker in *Eographis*. Moreover, *Racheliella* differs by having a subsutural band with spiral lirae and parasigmoidal growth lines. In addition, *Racheliella* is more high-spired than *Eographis* gen. nov. *Tofanella* Bandel, 1995 and *Cristalloella* Bandel, 1995 (including the subgenus *Wonwalica* Schröder, 1995) from the Late Triassic St. Cassian Formation and the Jurassic of Central Europe are more slender, have carinated teleoconch whorls and a stronger and coarser teleoconch ornament. *Camponaxis* Bandel, 1995 from the Late Triassic St. Cassian Formation is more slender and has a stronger and coarser teleoconch ornament. The Jurassic genera *Urlocella* Gründel, 1998 (considered to represent a synonym of the pyramidellid genus *Chrysallida* by Kaim 2004) and *Usedomella* Gründel, 1998 are much more slender and lack the fine axial ornament of *Eographis* (see also Gründel & Nützel 2013). The Jurassic genera *Conusella* Gründel, 1999 and *Reinbergia* Gründel, 2007 resemble *Eographis* in the relatively stout shape and in having a coaxial heterostrophic larval shell but differ in having an entirely smooth teleoconch. Schartiinae Nützel & Kaim, 2014 (= Ampezzanildidae *sensu* Bandel 1995) have a coaxial heterostrophic larval shell with strong axial ribs on the larval shell which is not the case in *Eographis*. *Trachoecus* Kittl, 1894 (Late Triassic St. Cassian Formation has an ornament of few but very strong axial ribs crossed by few but distinct spiral cords which is not the case in *Eographis*. *Carboninia* Bandel, 1996 from the Late Triassic St. Cassian Formation resembles *Eographis* in shape and in having coaxial heterostrophy but differs in having a smooth shell. The modern deep sea genera *Hyalogyra* Marshall, 1988 and *Hyalogyrina* Marshall, 1988 (Valvatoidea, Hyalogyrinidae) are similar but are usually more low-spired (except for *Hyalogyrina risoella* Warén & Bouchet, 2009 which is as high-spired as *Eographis*), have a smooth teleoconch and lack axial wrinkles on the early protoconch (*e.g.* Marshall 1988, Warén & Bouchet 1993). The Devonian *Palaeocarboninia* Bandel & Heidelberger, 2002 (Cornirostridae) resembles *Eographis* in shape and in having coaxial heterostrophy. However, *Palaeocarboninia* has a smooth shell. Moreover, due to preservation, the transition from protoconch to teleoconch cannot be seen. The Carboniferous genus *Heteroaclisina* Bandel, 2002b (Donaldinidae) also resembles *Eographis* in shape and in having coaxial heterostrophy. However,

Heteroaclisina has a dominant spiral ornament on the teleoconch.

***Eographis microlineata* Nützel & Ware sp. nov.**
Figure 6

LSID. urn:lsid:zoobank.org:act:0FB18883-FD88-4CF6-8158-057E0EF1A3AD

Types. – Holotype (PIMUZ 32911) and 10 paratypes (PIMUZ 32881, 32916, 32919, 32921, 32923, 32928, 32929, 32933, 32934, 32936, 32940, 32942, 32943).

Type horizon and locality. – Early Triassic, late Dienerian, from sample NAM101d, from about 6 m above the base of the Ceratite Marls (Ware *et al.* in press). Salt Range Pakistan, Nammal Nala.

Material. – See types.

Etymology. – For the fine teleoconch ornament of axial and spiral threads.

Diagnosis. – As for genus which is monotypic at present.

Description. – Teleoconch trochiform; holotype comprise *ca.* 3.5 whorl, 10.3 mm high, 0.9 mm wide; teleoconch whorls evenly convex, embracing slightly below periphery, ornamented with fine but distinct axial lirae and finer spiral lirae; axial lirae almost straight, orthocline, only slightly sinuous, distinctly curving forward at adapical suture and slightly prososcyrt on whorl face; base evenly convex, not demarcated from whorl face; protoconch flatly lying on apex, coaxial heterostrophic with immersed initial part; protoconch consisting of 1.4–1.5 rapidly increasing whorls, 0.33–0.37 mm in diameter; first part of visible protoconch with axial (radial) wrinkles, later largely smooth; transition to teleoconch abrupt with a ledge.

Infraclass Euthyneura
Superfamily Acteonoidea d'Orbigny, 1843
Family Tubiferidae Cossmann, 1895

Genus *Sinuarbullina* Gründel, 1997

Type species. – *Sinuarbullina ansorgi* Gründel, 1997, Jurassic, Bathonian, NE Germany, NW Poland.

***Sinuarbullina* sp.**
Figure 7

Material. – One specimen (PIMUZ 32883) from sample NAM101d, from Nammal Nala, about 6 m above the base of the Ceratite Marls (Ware *et al.* in press), Salt Range Pakistan, Early Triassic.

Description. – Shell slender, exposing about 4 whorls, *ca.* 0.9 mm high, 0.5 mm wide; spire gradate with distinct subsutural ramp; ramp almost horizontal to slightly inclined; whorl face concave below ramp and evenly convex at periphery; growth lines distinct, strongly sinuous, opisthocyrt below ramp, prosocyrt at periphery.

Remarks. – Although the protoconch is not preserved in the present specimen, the generic identity is beyond doubt because of the typical and characteristic teleoconch morphology. Shells like this were previously placed in the genus *Cylindrobullina* (see Gründel & Nützel 2012).

Discussion and conclusions

The studied sample derives from a limestone bed of Dienerian age with abundant ammonoids. The matrix between the ammonoids yielded thousands of tiny gastropods (< 2 mm) representing five species. The great majority (> 90%) are isolated larval shells and early juveniles of the soleniscid caenogastropod *Strobeus pakistanensis.* The other taxa are isolated larval shells of a trachyspirid (Neritimorpha) taxon, the small sized caenogastropod species *Coelostylina hydrobiformis* sp. nov. as well as the heterobranchs *Eographis microlineata* gen. nov., sp. nov. and *Sinuarbullina* sp.

The studied gastropod assemblage has a low diversity comprising only 5 species. It shows a pronounced faunal homogeneity with a strong dominance of *Strobeus pakistanensis.* The high number of isolated larval and early juvenile shells indicates that this assemblage did not form under normal marine living conditions before transport by storm but that at least one environmental parameter hindered larger growth of the juveniles or a successful metamorphosis of the larvae. Poor living conditions on the sea floor – maybe caused by oxygen deficiency – are thus reflected by larval fall (no metamorphosis possible) or high mortality (high abundance of early juveniles). However, the small-sized species could have been adapted to low oxygen concentrations. The small size does not result from *post mortem* size-sorting because larger ammonoids and shell fragments are present in the studied sample which represents a poorly sorted tempestite. The fact that ammonoids are also abundant while fossil remains of larger benthic animals seem to be absent also argue for poor living conditions on the sea floor and that the main source for the fossils was the plankton and the nekton. A similar cephalopod-microgastropod association – though without storm-generated transport – was reported from the Early Carboniferous Ruddle Shale in Arkansas, USA (Nützel & Mapes 2001, Mapes & Nützel 2009). In

this case primarily pyritized cephalopods and tiny gastropods (< 2 mm) occur abundantly in black shale whereas larger benthic animal are almost entirely absent. This has been interpreted as a mixture of larval fall and nektonic organisms and the almost entire lack of benthos as result of bottom water oxygen deficiency. The present sample can be interpreted as an analogue facies in the calcareous realm. However, the presence of many clearly post-larval, mostly juvenile gastropods suggests that oxygen concentration were sufficient to permit at least temporarily a short live span on the bottom. The tiny gastropod shells reported from the Smithian of north-eastern Vietnam by Kaim *et al.* (2014) have also been interpreted as isolated larval conchs or early juveniles of taxa having mostly planktotrophic larval development. This assumption was based on the small size of the specimens (smaller than 1 mm) and the fact that the initial whorl is present in most specimens showing that the apical portions of gastropods are present (as in the case of the gastropods studied here). The small size of these gastropods is no evidence for the Liliput Effect which proposes a generally small adult size after the extinction event (see *e.g.* Fraiser & Bottjer 2004; Fraiser *et al.* 2005, 2011; Brayard *et al.* 2010, 2011, 2015 for discussion).

A hallmark of the present fossil assemblage is the excellent preservation of the gastropods including protoconchs and micro-ornaments. Good protoconch preservation in Early Triassic gastropods has only been reported from the Smithian Sinbad Limestone of Utah, USA (Batten & Stokes 1986, Nützel 2005, Nützel & Schulbert 2005), the Chinese Dayie Formation (Hua Zhang *et al.* 2003), the Early Triassic of Far East Russia (Kaim 2009), the Olenekian of Vietnam (Kaim *et al.* 2014) and from a silicified Griesbachian fauna from Spitsbergen (Foster *et al.* 2017). The total number of described Early Triassic gastropod species is very low and most species are based on poorly preserved material lacking protoconch preservation. However, in many gastropod species the knowledge of the protoconch is crucial for a correct classification and therefore also for the analyses of evolutionary lineages at critical intervals such as the end-Permian mass extinction event and subsequent recovery. Therefore, the present assemblage, being the first record of Dienerian gastropods with well-preserved protoconchs, adds important information about gastropod evolution after the end-Permian mass extinction event.

The characteristic isolated trachyspirid larval shells in the present fauna show that this Palaeozoic group survived the mass extinction and its presence in the Dienerian bridges the Lazarus-gap between the Permian (Nützel *et al.* 2007, Pan & Erwin 2002) and the Late Triassic (Bandel 2007, as Naticopsidae). Neritimorphs with this type of axially ribbed larval shells have not been reported from post-Triassic strata so that Trachyspiridae probably became extinct in the Late Triassic, possibly during the end-Triassic mass extinction event.

The highly abundant larval and juvenile shells of *Strobeus pakistanensis* belong to the 'subulitoid' family Soleniscidae which was diverse and widespread in the Late Palaeozoic. The survival of this group into the early Triassic has repeatedly been shown at a global scale (Batten & Stokes 1986, Nützel 2005, Wheeley & Twitchett 2005, Kaim 2009, Kaim *et al.* 2013) but its relationships to younger smooth-shelled caenogastropods remain unclear.

The caenogastropod genus *Coelostylina*, represented by the new species *C. hydrobiformis*, has previously been reported from the Permian and the Early Triassic with a few species (see Kaim *et al.* 2013 for discussion). According to the current state of knowledge this genus ranges from the Middle Permian to the Jurassic. In the Early Triassic, the present specimens of *Coelostylina* are the best preserved ever recorded. They have orthostrophic initial whorls probably representing a smooth larval shell. This information is crucial because small high-spired shells have evolved in several gastropod groups. For instance Heterobranchia and Caenogastropoda commonly have homoplastic teleoconch morphologies but based on the present well-preserved material it can be excluded that *C. hydrobiformis* is a member of the Heterobranchia.

The presence of the new genus *Eographis* is an important feature of the studied fauna. As discussed above, its placement in Hyalogyrinidae seems to be the best solution although "lower heterobranchs", both modern and fossil are an unresolved group with a spotty fossil record and a lack of molecular and anatomical studies in many living taxa. The possibility that *Eographis* belongs to the heterobranch Pyramidelloidea lineage (*e.g.* it resembles modern genera such as *Chrysallida* to some degree) cannot be ruled out. However, since Pyramidellidae of this relation commonly have a tooth in the aperture and differ widely in teleoconch ornament this relationship is seen as unlikely. Moreover pyramidellids lack axial wrinkles on the protoconch. It is unclear whether *Eographis* could also belong to Cornirostridae (also marine Valvatoidea) based on its resemblance to the Late Triassic *Carboninia*. However, shell shape in this group is usually depressed trochiform and distinctly umbilicated.

Eographis has coaxial heterostrophy which is also present in the mathildoid family Tofanellidae. However, the teleoconch of *Eographis* differs considerably from most Mathildoidea including tofanellids in shell shape and ornamentation. The present material of *Eographis* represents the first Early Triassic example of a protoconch with coaxial heterostrophy. There are a few Palaeozoic (Devonian, Carboniferous) examples for gastropods with coaxial heterostrophy (Bandel 2002b; Bandel & Heidelberger 2002) which could actually also belong to Hyalogyrinidae or Cornirostridae. These Palaeozoic genera, *Heteroaclisina* and *Palaeocarboninia*, may be closely related to *Eographis*. This group of ancient lower heterobranchs may

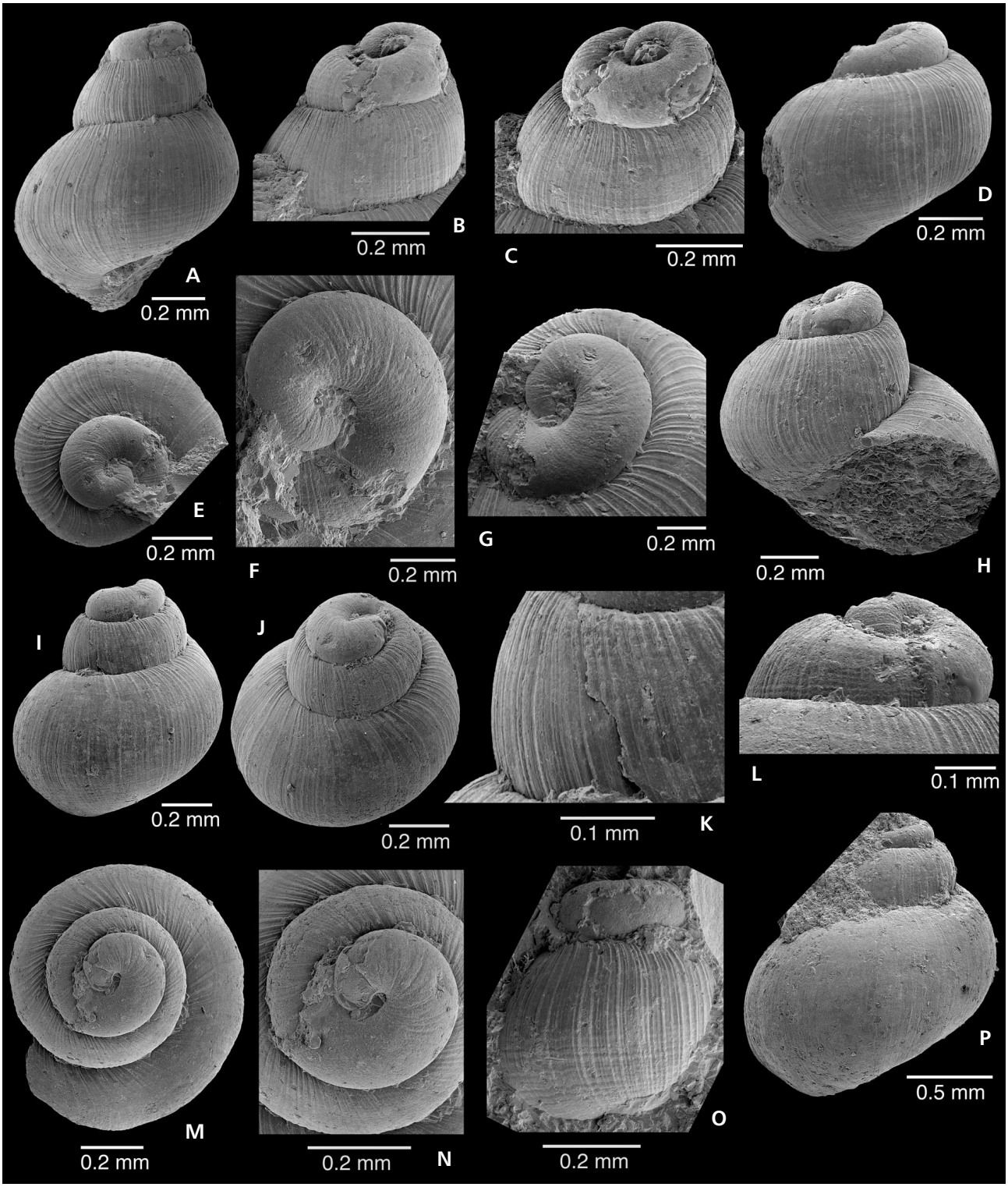

Figure 6. *Eographis microlineata* sp. nov.; A–C – holotype, PIMUZ 32911; D–G – paratype, PIMUZ 32916; H, I – paratype, PIMUZ 32919; J–N – paratype, PIMUZ 32942; O – paratype, PIMUZ 32923; P – paratype, PIMUZ 32943.

include evolutionary lineages that gave rise to modern groups such as Mathildoidea. The high age of this group resembling living ectobranchs supports statements that living Ectobranchia (Hyalogyrinidae, Valvatidae, Cornirostridae and Xylodisculidae) represent the first extant offshoot of the Heterobranchia (Haszprunar *et al.*

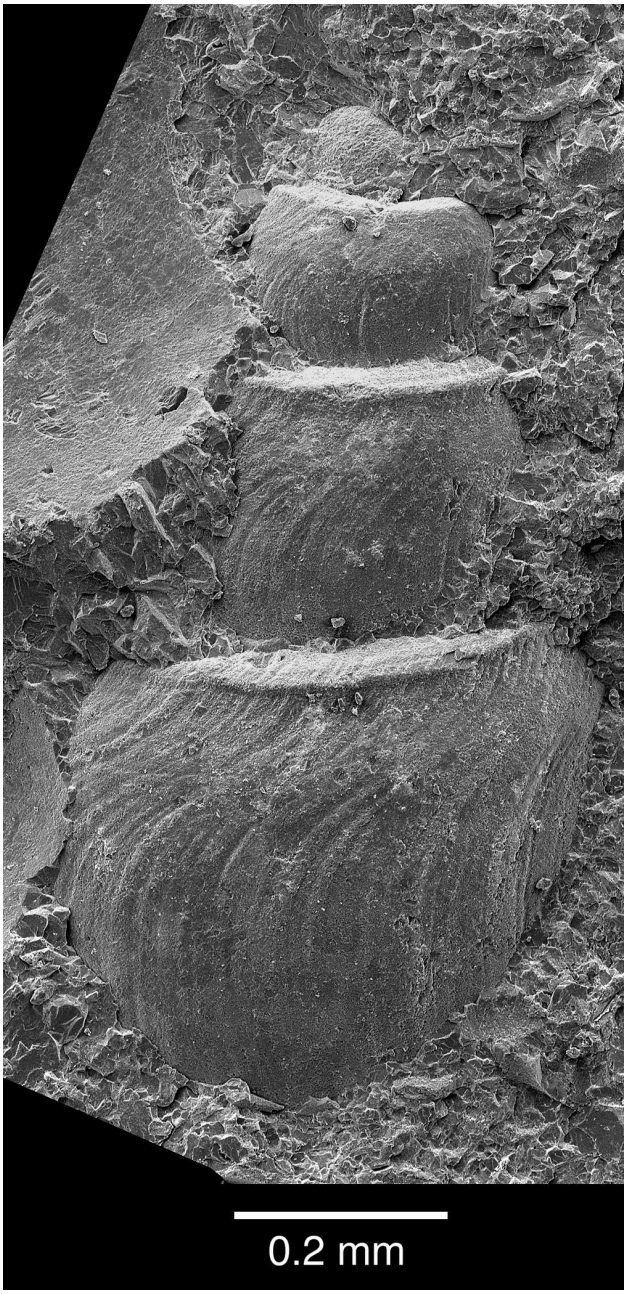

Figure 7. *Sinuarbullina* sp., PIMUZ 32883.

2011). The earliest occurrence of the diverse superfamily Mathildoidea as evidenced by the knowledge of the protoconch are from the Late Triassic. The protoconch of *Promathildia spirocostata* Batten & Stokes, 1986 from the Smithian Sinbad Limestone is unknown and its teleoconchs is not particularly typical of *Promathildia* (Nützel 2005). Mathildoidea are richly diversified throughout the Mesozoic and are still diverse today (Bandel 1995, Bieler 1995, Gründel & Nützel 2013).

Sinuarbullina sp. in the present collection is a typical representative of this genus. The oldest known species is *Sinuarbullina yangouensis* (Pan, Erwin, Nützel & Xiang-shui, 2003) from the Early Triassic of China (Pan *et al.* 2003) and the Griesbachian of Spitsbergen (Foster *et al.* 2017). *Sinuarbullina convexa* (Batten & Stokes, 1986) from the Smithian Sinbad Limestone of Utah is also similar (see also Nützel 2005, Nützel & Schulbert 2005, Gründel & Nützel 2012). So far, no members of *Sinuarbullina* or related heterostrophic genera of the tubiferid/cylindrobullinid-group have been reported from the Palaeozoic so that the entire group seems to have originated in the earliest Triassic, thus providing additional evidence for the Early Triassic heterobranch turnover (Nützel 2005, Gründel & Nützel 2012).

Of the five genera present in the studied Dienerian assemblage, three are holdovers from the Palaeozoic (*Strobeus*, *Coelostylina*, trachyspirid) and two originate in the Early Triassic (*Eographis*, *Sinuarbullina*). The status of *Coelostylina* is in this respect unsafe because its Permian members are not sufficiently known. *Eographis* and *Sinuarbullina* represent the earliest occurrences of important heterobranch groups, indicating a considerable turnover within Heterobranchia during the aftermath of the end-Permian mass extinction event. Most of the present gastropods had planktotrophic larval development providing further evidence against the hypothesis that the end-Permian mass extinction event selected against larval planktotrophy (Valentine 1986, see Nützel 2014 for further discussion).

Acknowledgements

We thank Andrzej Kaim (Warszawa), Winston Ponder (Sydney) and Anders Warén (Stockholm) for helpful discussions about the systematic placement of the new genus *Eographis*. Stefano Monari (Padova) and Peter Wagner (Lincoln) are acknowledged for their helpful reviews. AN acknowledges support by the Deutsche Forschungsgemeinschaft (Grant NU 96/6-1, 6-2). The study of the Early Triassic record in the Salt Range was supported by the Swiss National Science Foundation (project SNF 135446 to HB).

Data archiving statement

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